

Genetic Variation for Agronomic and Fiber Properties in an Introgressed Recombinant Inbred Population of Cotton

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ABSTRACT

Genetic variation available for the improvement of fiber properties is restricted in commercial upland cotton (*Gossypium hirsutum* L.). Resources for fiber improvement exist in *G. barbadense* L., but introgression of traits has been a limited success. The objectives of this study were to investigate the genetic variation and heritability of agronomic and fiber traits within a diverse recombinant inbred line (RIL) population created with a stable introgressed parent. The population ($n = 98$ lines) had as its parents NM24016, a stable *G. hirsutum* line with significant introgression from *G. barbadense*, and TM1, the *G. hirsutum* genetic standard. Yield, plant height, boll size, lint percentage, and fiber length, strength, micronaire, and elongation were measured in randomized, complete block tests at Las Cruces, NM, and Maricopa, AZ, in 2001 and 2002. Genotype coefficients of variation (CV) were highest for plant height and boll size. Among fiber traits, fiber length and micronaire produced the highest genotype CVs. Most traits (fiber elongation excepted) exhibited high broadsense heritability, ranging from 0.69 for lint yield to 0.92 for 2.5% span length. Transgressive segregants were identified for most traits. Fiber strength and 2.5% span length were favorably correlated ($r = 0.59$, $P = 0.001$) as were 2.5% span length and micronaire ($r = -0.47$, $P = 0.001$). The NM24016/TM1 RIL population presents valuable genetic variation for fiber quality improvement efforts in *G. hirsutum*.

HISTORICALLY, four species of *Gossypium* have been cultivated for fiber (Brubaker et al., 1999). Of these species, the tetraploid *G. hirsutum* and *G. barbadense* currently dominate commercial cotton production, with *G. hirsutum* accounting for over 90% of the production. *Gossypium hirsutum* and *G. barbadense* differ significantly in their agronomic and fiber attributes and their commercial end uses. The higher yield potential and broader environmental adaptability evident in *G. hirsutum* have been increased through breeding and genetic manipulation. Similarly, the superior fiber attributes of the *G. barbadense* species have been emphasized in the development of commercial cultivars in that species. Production of *G. barbadense* has been limited not only by the specialty nature of its high quality fiber but also by its lower yield potential, greater heat sensitivity, and longer growing period. Although *G. hirsutum* dominates fiber production, modern spinning techniques and end uses have created demands for improved fiber quality in that species (McCreight, 1992; Felkner, 2001).

Traits that have been identified as desirable include greater fiber strength, greater length, increased uniformity of length, and finer fiber at maturity (McCreight, 1992; Deussen, 1992). Of the above, commercial *G. barbadense* possesses greater fiber lengths, strengths, and fineness (micronaire) than currently available in *G. hirsutum*.

In recent years, there has been a growing recognition of the limited genetic diversity of elite commercial germplasm of both species and a growing concern about genetic vulnerability (Bowman et al., 1996). This genetic impoverishment may have resulted from numerous sources and activities. In both species, the process of domestication is thought to have dramatically narrowed the germplasm base (Brubaker et al., 1999). Early and modern improvement efforts further narrowed this base. May (2000) reported that intensive selection imposed to maximize yield and adaptation, along with selection for early maturity, has eliminated substantial variation from elite *G. hirsutum* germplasm pools. In *G. barbadense*, only a very small portion of the primitive and obsolete germplasm exhibits the highly desirable fiber characteristics that are common to modern commercial cultivars (Percival, 1987). This genetic resource has been further narrowed by the transfer of a subset of the high fiber quality Sea Island cottons to Egypt for the development of the modern Giza cultivars and the subsequent transfer of a subset of Egyptian cultivars to the USA for the development of modern Pima cultivars (Smith et al., 1999). The genetic narrowness of the commercial germplasm has been cited as a contributing factor for the perceived plateau in yield and fiber improvement in recent years. As a result of concerns regarding genetic vulnerability and improvement plateaus, there has been renewed interest in interspecific introgression and use of related species as sources of genetic variation in improvement efforts (May et al., 1995).

Recognition of the complementary attributes of *G. hirsutum* and *G. barbadense* has led to interspecific hybridization and introgression efforts in these species that predate the current concerns regarding genetic vulnerability and yield plateaus. Despite past interspecific hybridization efforts, modern cultivars display few traits that can be attributed to introgression. Efforts to improve *G. hirsutum* or *G. barbadense* through introgression have been hindered by genetic breakdown in segregating interspecific breeding populations (Stephens, 1949). Infertility and distorted preferential segregation have been prevalent. Rhyne (1958) reported that the number of recombinants occurring in an interspecific backcross program were greatly inferior to the expected number. Reinisch et al. (1994) reported strongly distorted segregation of molecular markers in early generations, and Jiang et al. (2000) reported skewed

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transmission in advanced generations of interspecific hybrids. All of the above have made the recovery of desirable attributes in introgressed populations problematic and has lessened the utility of interspecific populations in applied molecular mapping, quantitative trait loci (QTL) analyses and marker-assisted selection efforts. Despite the above, genetically stable lines that exhibit significant combinations of *G. hirsutum* and *G. barbadense* chromatin have been developed after lengthy cycles of breeding and selection (Tatineni et al., 1996; Cantrell and Davis, 1993). Use of a stabilized introgression line as a parent in the creation of diverse populations should yield genetic variation that is greater than an intraspecific *G. hirsutum* population yet not have the distorted segregation common to pure *G. hirsutum* by *G. barbadense* hybrid populations.

In the present study, the stabilized introgression line NM24016, displaying significant introgression from *G. hirsutum* and *G. barbadense* (Cantrell and Davis, 2000; Cantrell et al., 2000), was crossed to the *G. hirsutum* standard TM-1 to create a population of introgressed recombinant inbred lines. The objectives of the study were to determine the genetic variation present in the introgressed RIL population for agronomic and fiber quality traits, their heritability, and the utility of the population in cotton improvement efforts.

MATERIALS AND METHODS

Genetic Materials

Recombinant inbred lines were generated from the cross of NM24016 with TM-1, made in 1994. NM24016 is an inbred line with the interspecific pedigree, H12156/2/77-505/Russian 5904 (Cantrell and Davis, 2000). Deliberate selection was practiced for traits derived from both *G. hirsutum* and *G. barbadense* in the development of NM24016 to achieve a stable introgressed line. Approximately 63% of the NM24016 genome sampled with DNA markers was homozygous for typical *G. hirsutum* alleles and 37% was homozygous for typical *G. barbadense* alleles (Cantrell and Davis, 2000). The TM-1 parent serves the research community as the genetic standard for *G. hirsutum* and is derived from 'Deltapine 14' (Kohel et al., 1970). An initial 118 F₂ plants from the NM24016/TM-1 cross were manually self-pollinated and advanced to the F_{5,6} generation by single-boll descent, accompanied by manual selfing without selection. The bulked F_{5,7} seed was utilized in the 2-yr field experiment. Of the original 118 lines, 98 F_{5,7} had adequate open pollinated seed for evaluation. Individual F_{5,7} progenitor rows were maintained by bulk manual selfing to ensure purity for future genetic analyses and potential distribution for the RILs.

Experimental Design

The 98 RI lines and their two parents were grown in replicated tests at Las Cruces, NM, and Maricopa, AZ, in 2001 and 2002. Las Cruces is typical of cooler high-elevation (>1000 m) irrigated cotton production areas of the arid southwestern USA, whereas Maricopa is characteristic of lower elevation (<200 m) growing environments of that region that often experience high temperature extremes. The soil type at Las Cruces is a Glendale loam (fine-silty, mixed, superactive, calcareous, thermic Typic Torrifluvents, pH = 8.0). Maricopa tests were grown on a Casa Grande sandy loam (fine-loamy, mixed, superactive, hyperthermic Typic Natrargids). Tests at both

locations in both years were randomized, complete block designs. Tests at Maricopa included four replicates in both 2001 and 2002. Tests at the Las Cruces locations included three replicates in 2001 and four replicates in 2002. Individual plots at Maricopa and Las Cruces were two rows, 1.01 m apart, 12.2 m long in 2001 and 10 m long in 2002. All plots were grown under flood irrigation conditions with standard agronomic and pest control practices for the respective locations.

All plots were machine harvested with a two-row harvester. Before machine harvesting, a standard number of bolls (25 bolls at Las Cruces and 50 bolls at Maricopa) were hand-harvested from all plots for determination of lint percentage, boll size, and for fiber analyses. Lint percentage was calculated from the boll samples by weighing seed-cotton, ginning samples, weighing the seed and fiber components, and expressing the fiber component as a percentage of the total sample weight. Boll size was calculated by dividing the seed-cotton weight of a boll sample by the number of bolls comprising the sample. At the Maricopa location, a seed index was obtained by weighing 100 seed from each ginned boll sample. Seed-cotton yield per plot from machine harvesting was transformed to lint yield with the lint percentages calculated from corresponding boll samples. Approximately 13 g of fiber from each boll sample was used for determination of fiber properties. Fiber analyses for all samples from the Maricopa location were performed by Star Lab (Knoxville, TN) using individual instrumentation. Fiber analyses of samples collected at Las Cruces were performed using individual instrumentation by a laboratory at that location. Fiber properties were measured as follows:

1. Fiber length, reported in millimeters, was measured for the upper 2.5% span length (2.5% SL) and the 50% span length (50% SL) with a digital fibrograph.
2. Fiber uniformity (UR) was calculated as the ratio of the 50 to 2.5% span lengths (50/2.5), and was expressed as a percentage.
3. Fiber strength (T_i), measured by a stelometer, is the force (cN) necessary to break a fiber bundle with the jaws of the instrument set 3.2 mm apart.
4. Fiber elongation (E_1) was measured as the percentage elongation of the fiber bundle before breakage with the stelometer jaw gap set at 3.2 mm.
5. Micronaire, measured on a fibronaire instrument, is an indirect measure of fiber fineness. Micronaire measures the resistance to airflow created by a standard weight of fiber in an enclosed cylinder.

At the Maricopa location, a single-row plant height measurement was made in each plot of the replicated tests at the time of harvest in 2001 and 2002.

Statistical Analyses

Genotype means, ranges, and standard errors of the various traits were calculated across locations and years for the RIL lines and their parents from raw data. Parental midparent values were calculated, and deviations of the RIL population trait means from their midparent values were tested by paired *t* tests. Since the distribution of RIL trait means in the population were of interest, across location and year means of non-transformed data were tested for normal distribution, skewness, and kurtosis by the UNIVARIATE procedure of SAS (SAS Institute, 2000).

Before analyses of variance, the Box et al. (1978) power transformation series was tested on all dependent variable data in an effort to achieve error variance homogeneity, stabilize variances among fixed effects, and to attain normality. On the basis of results from these tests, boll size data were

Table 1. F values and significance levels of fixed sources of variation in the combined analyses of variance of 98 RI lines and their parents for agronomic and fiber traits, over years (2001 and 2002) and locations (Maricopa, AZ, and Las Cruces, NM).

	Den	Lint				Length				Plant	
Source	DF	Boll size	Percentage†	Yield	Micronaire	Elongation	Strength	50% SL	2.5% SL	Uniformity	Height‡
Year (Y)	11	1.82ns	278.29***	14.21**	0.04ns	5777.92***	17.02**	50.51***	19.38**	51.12***	1.48ns
Location (L)	11	802.86***	6689.76***	70.35***	2.02ns	2192.38***	155.17***	14.51**	15.25**	3.05ns	
Y×L	11	82.26***	284.79***	7.92*	19.32**	3868.48***	19.14**	19.32**	0.91ns	81.77***	
Genotype (G)	1067	23.29***	35.00***	10.30***	25.23***	6.83***	14.05***	7.86***	27.77***	9.62***	8.21***
G×Y	1067	1.92***	1.48**	2.09***	1.69***	3.37***	1.23ns	1.44**	1.75***	1.39**	1.23ns
G×L	1067	2.27***	2.93***	2.97***	2.07***	3.48***	1.41**	1.13ns	1.73***	1.07ns	
G×Y×L	1067	1.06ns	0.98ns	1.73***	1.24ns	2.25***	1.30*	0.97ns	1.02ns	1.07ns	

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† Rep(Y×L) for lint percentage was estimated to be zero and therefore all sources of variation were tested with the error variance with a Den DF of 1078.

‡ Plant height measurements were made only at the Maricopa location. The Den DF for year was 6 and for genotype and G×Y was 582.

transformed by the square of data, plant height data were transformed by the log of data, fiber elongation (E_l) and strength (T_l) were transformed by the reciprocal square root of data, fiber length data (2.5 SL and 50 SL) were transformed using the reciprocal square transformation, and the ratios lint percentage and length uniformity were transformed by the arcsine square root transformation. Analyses of variance of transformed data were conducted by the SAS Mixed Procedure (SAS Institute, 2000), in which genotypes, locations, and years were considered as fixed variables and replication within locations and years was considered as a random variable. Estimates of variance components were calculated by the VARCOMP procedure of SAS and the restricted maximum likelihood method (REML). All variance component estimates were transformed to their respective coefficients of variation (CV%) to allow direct comparisons between traits. Broad-sense heritability (h^2) estimates were calculated by variance components as described by Fehr (1987).

RESULTS

Genetic Variability and Heritability

Differences among RI lines (genotypes) were observed for all traits measured (Table 1). Location and year differences were also observed for most traits, as were significant genotype × year (G × Y) and genotype × location (G × L) interactions. Genotypic coefficients of variation (CV) were largest for the agronomic traits plant height and boll size (Table 2). Among fiber traits, the larger genotypic CVs were obtained for 2.5% SL and 50% SL fiber length and for micronaire. The lowest levels of genotypic variation within the RI line (RIL) population were obtained for fiber length uniformity

and elongation. Genotype × year interaction CVs for the agronomic traits boll size and plant height exceeded G × Y interaction CVs for fiber traits. Similarly, G × L and G × Y × L interaction CVs for boll size and lint yield exceeded the G × L and G × Y × L CVs for fiber traits. With the exception of fiber elongation, broad-sense heritability estimates for traits measured in the RIL population were high, ranging from 0.69 for lint yield to 0.92 for 2.5% span length. Fiber elongation, which displayed a low genotype CV and relatively larger interaction CVs, exhibited a heritability of 0.39.

Trait Means and Distributions

The distribution of RIL means for the agronomic traits boll size, lint percentage, and lint yield were normally distributed (Table 3). However, the RIL distribution for boll size appeared to be shifted toward the smaller boll size of the NM24016 parent, as indicated by a RIL population mean that was lower than the midparent value (Table 4). The RIL population means for lint percentage and lint yield did not differ from their respective midparent values. Transgressive segregate lines occurred for both high and low lint percentage, with approximately 5% of the lines exceeding the high lint percentage parent NM24016 (Fig. 1a). Three RI lines differed significantly from the higher yielding TM-1 parent and appeared to be transgressive segregate lines for that trait (Fig. 1b). The distribution of plant height means deviated significantly from normality and a large skewness value was obtained within the RIL population. Approximately 25% of the RIL population

Table 2. Coefficients of variation for variance components influencing the agronomic and fiber traits of the NM24016/TM-1 RIL cotton population, and the broadsense heritabilities of those traits.

Variance component	Coefficients of variation									
	Boll size	Lint Percentage	Yield	Micronaire	E1	T1	50% SL	2.5% SL	Uniformity	Plant height
Year (Y)	0.00	0.00	2.39	0.00	16.61	0.00	4.16	2.43	0.38	6.55
Location (L)	30.41	6.29	7.57	0.00	0.00	2.93	0.00	2.14	0.00	.
Y×L	10.00	1.86	3.52	0.55	24.66	1.46	4.03	0.00	1.19	.
Genotype (G)	14.87	3.09	5.28	4.33	1.66	2.47	4.61	5.92	1.25	65.20
G×Y	4.26	0.55	1.63	0.93	1.46	0.00	1.66	1.37	0.38	16.82
G×L	4.97	1.10	3.00	1.14	1.54	0.40	0.65	1.35	0.10	.
G×Y×L	2.15	0.17	3.42	0.83	2.10	0.69	0.00	0.00	0.18	.
Replication(Y×L)	2.70	0.00	2.50	0.25	0.77	0.63	1.82	1.45	0.31	18.27
Error	12.77	2.11	7.69	3.49	3.88	2.67	7.13	4.57	1.69	69.82
Heritability (h^2)	0.87	0.90	0.69	0.90	0.39	0.90	0.82	0.92	0.86	0.85

Table 3. Tests for normal distribution, skewness, and kurtosis of RI line means within the NM24016/TM-1 RIL population.

Traits	W ² test for normality		
	(P values) [†]	Skewness	Kurtosis
Boll size	>0.25	0.278	0.016
Lint percentage	>0.25	0.055	0.043
Lint yield	>0.25	0.461	0.450
Plant height	0.009	0.630	0.115
Micronaire	0.083	-0.267	-0.015
E ₁	0.017	0.204	0.682
T ₁	>0.25	0.539	0.371
0.50-Span length	>0.25	0.562	1.662
0.025-Span length	>0.25	-0.092	0.878
Length uniformity	>0.25	0.023	1.005

[†] Cramer-von Mises goodness of fit test for normal distribution.

exceeded the taller NM24016 parent in height and therefore were transgressive segregate lines for taller plant height (Fig. 1c).

The RI lines were normally distributed for fiber strength, and their population mean did not differ from the midparent value. A larger skewness value suggested some skew among the RI lines toward higher fiber strength. Approximately 20% of the RI lines possessed fiber strengths equivalent to the high strength NM24016 parent, and four lines appeared to be transgressive segregates for high fiber strength (Fig. 1d). None of the traits associated with fiber length (50% SL, 2.5% SL, and uniformity) departed from normality nor had they population means that differed from midparent values. However, higher kurtosis values were observed for all three traits. Although approximately 15% of the RI lines were transgressive segregates for shorter 2.5% span length; transgressive segregate lines for longer fiber length also occurred (Fig. 1e). Over 20% of the RIL population produced 2.5% span lengths equivalent to or better than the longer fibered NM24016 parent. The distribution of micronaire means among the RI lines departed from normality and the RIL population mean was significantly lower than the midparent value. Approximately 14% of the RI lines appeared to be transgressive segregates for lower micronaire (Fig. 1f). The distribution of RI lines for fiber elongation appeared to deviate from normality. However, there was actually very little differentiation among RI lines for elongation. The parents did not differ from each other for elongation, and large standard errors were obtained for individual lines (data not shown).

Phenotypic Correlations

A number of phenotypic correlations were observed among the traits of the RIL population. Lint percentage was observed to be positively associated with lint yield and micronaire and negatively associated with 2.5 and 50% span length (Table 5). Lint yield, in addition to being associated with lint percentage, was also positively associated with plant heights and micronaire. Among fiber traits, fiber strength was positively associated with 2.5 and 50% span lengths. Micronaire was negatively associated with 2.5% span length but positively associated with fiber length uniformity. Fiber length uniformity was negatively associated with 2.5% span length.

DISCUSSION

Significant genotypic variation occurred in the NM24016/TM-1 RIL population for all traits, with greater variation occurring for the agronomic traits boll size and plant height (Tables 1 and 2). Among fiber traits, greater genotypic variation occurred for the traits 2.5 and 50% span lengths and for micronaire. All traits, with the exception of fiber elongation, exhibited high broadsense heritabilities. Fiber strength, while producing a lower genotype coefficient of variation also produced lower interaction and error CVs, leading to a high heritability for that trait.

The variation observed within the RIL population has practical applications for fiber improvement efforts. The introgressed NM24016 parent, with a 2.5% span length of 31.7 mm and stelometer strength of 23.0 cN, possesses superior fiber attributes. The RIL population included a number of lines possessing fiber strengths equivalent to NM24016, and three to four outstanding transgressive segregate lines possessing fiber strengths in excess of 24.0 cN. Although 15% of the RI lines exhibited transgressive segregation for shorter 2.5% span lengths, 20% of the lines were equivalent to or better than the superior NM24016 parent for length. High micronaire is an undesirable trait in a mature fiber, resulting in price discounts (Calhoun and Bowman, 1999). The NM24016 parent possessed a lower, more desirable micronaire value, and approximately 14% of the RI lines were transgressive segregates for micronaire values lower than NM24016.

Table 4. Across locations (Las Cruces, NM, and Maricopa, AZ) and years (2001 and 2002) means, ranges, midparent values, and *t* tests for deviation of RIL population means from midparent values for agronomic and fiber traits within the NM24016/TM-1 RIL population.

Traits	RIL population		Parent means		Midparent	<i>t</i> Ho: mean-MP = 0
	Mean	Range	NM24016	TM-1		
Boll size (g boll ⁻¹)	4.84	4.07–5.98	4.38	6.05	5.22	-6.64**
Lint percentage	34.0	30.0–40.0	36.0	33.0	35.0	-1.56
Lint yield (kg ha ⁻¹)	1137	870–1593	1015	1357	1186	-2.15
Plant height (m)	1.15	0.92–1.47	1.12	1.03	1.08	2.04
Micronaire	4.40	3.64–5.03	4.26	4.91	4.59	-5.81**
E ₁	6.24	4.85–7.40	5.79	6.40	6.10	0.94
T ₁ (cN)	21.7	19.6–25.5	23.0	20.2	21.6	0.57
0.50-Span length (mm)	14.7	13.5–16.3	15.0	14.5	14.7	-2.38*
0.025-Span length (mm)	30.7	27.9–33.8	31.8	30.2	31.0	-1.90
Length uniformity	0.48	0.44–0.51	0.48	0.48	0.48	-1.23

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

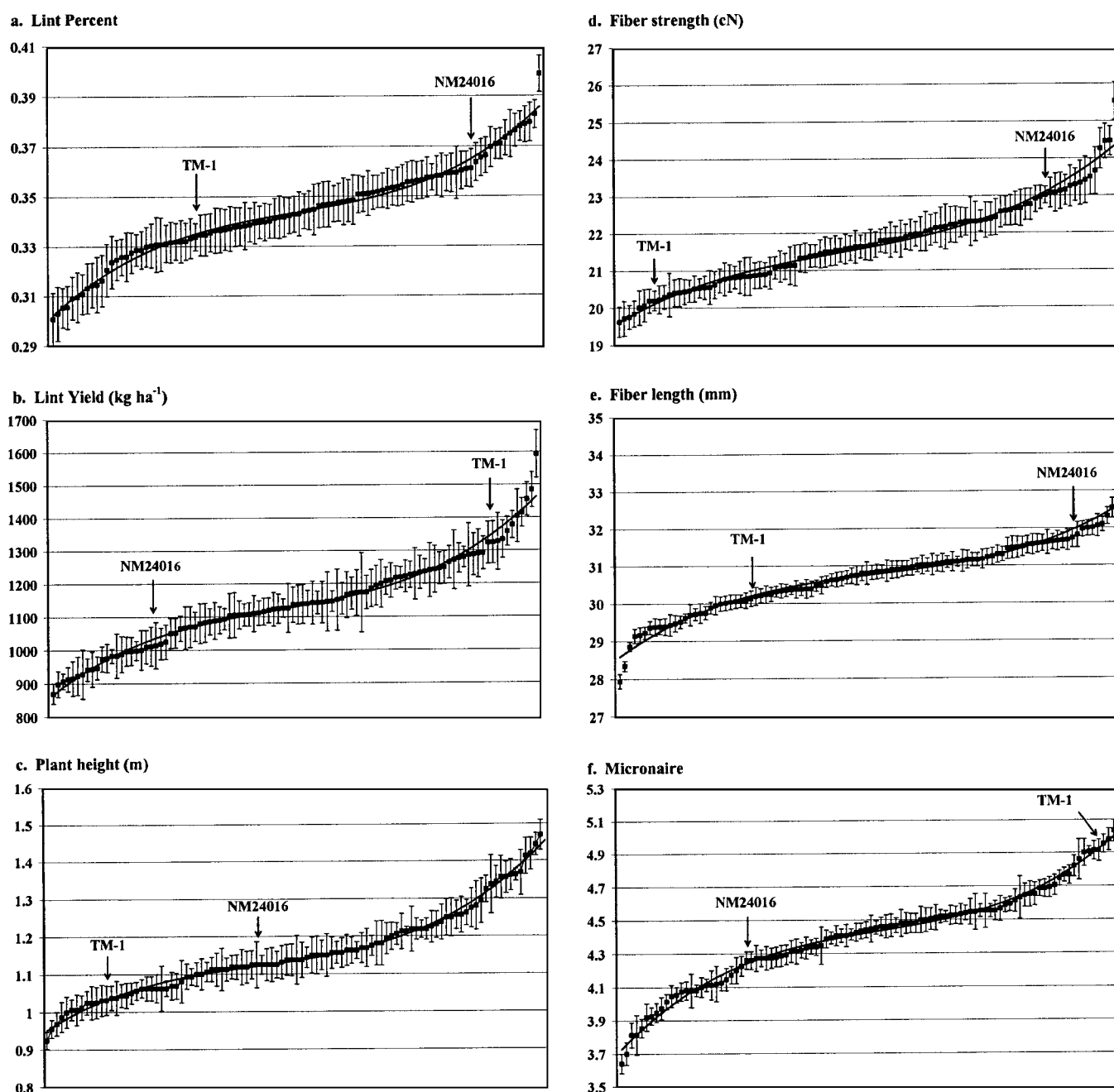


Fig. 1. Across locations and years means and standard errors for the 98 NM24016/TM-1 RI cotton lines and their parents for the traits a) lint percentage, b) lint yield, c) plant height, d) fiber strength, e) 2.5 SL fiber length, and f) micronaire. Tests were conducted at Maricopa, AZ, and Las Cruces, NM, in 2001 and 2002.

Phenotypic correlations among traits of the RIL population suggest that individual lines can be identified within the population for the simultaneous improvement of multiple fiber traits. The positive correlation of 2.5 and 50% span lengths with fiber strength suggests that lines with superior length and strength can be identified in the population. In fact, 12 RILs have been identified that possess fiber strengths and 2.5% span lengths equal to or greater than the superior fibered NM24016 parent (data not shown). Lower micronaire being desirable, the negative phenotypic correlation between micronaire, and 2.5% span length suggests that

lines within the population can be identified for simultaneous improvement of these two traits. Examination of the population reveals 14 lines possessing micronaire values lower than or equal to NM24016 and 2.5% span lengths greater than or equal to NM24016. Taken together, the above phenotypic correlations lead to the speculation that the superior fiber length, strength, and micronaire attributes of the NM24016 parent might not have segregated in a completely independent, random manner within the RIL population. Not surprisingly lint percentage, which is a component of lint yield (Calhoun and Bowman, 1999), was positively correlated with yield.

Table 5. Phenotypic correlations among agronomic and fiber traits of 98 RI lines, averaged across the Las Cruces, NM, and Maricopa, AZ, locations in the years 2001 and 2002.

Traits	Boll size	Lint percentage	Lint yield	Plant height	Fiber				
					Micronaire	Elongation	Strength	Length 50%SL	Length 2.5%SL
Lint percentage	−0.18								
Lint yield	0.03	0.56***							
Plant height	0.00	−0.04	0.30**						
Micronaire	0.13	0.47***	0.34***	0.09					
Elongation	−0.04	−0.08	−0.02	0.10	−0.05				
Strength	0.18	−0.09	0.09	−0.10	−0.19	−0.22*			
Length (50%SL)	0.22*	−0.30**	0.06	0.13	−0.06	−0.06	0.59***		
Length (2.5% SL)	0.19*	−0.44***	−0.08	0.07	−0.47***	−0.17	0.48***	0.73***	
Length uniformity	−0.01	0.26**	0.19	0.05	0.60***	0.17	0.03	0.18	−0.54***

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

However, negative correlations of lint percentage with 2.5 and 50% span lengths did not translate into negative correlations between the latter two fiber length traits and lint yield. The lack of the often observed negative correlation of lint yield with various fiber quality attributes (Meredith, 2003) suggests that lines can be identified within the RIL population for simultaneous improvement of yield and fiber quality.

Agronomic traits of the RIL population were less desirable for agronomic improvement. Taller plant heights at maturity have been associated with later plant maturity and can present harvest difficulties. In this regard, the large portion of the RI lines (25%) exhibiting transgressive segregation for taller plant heights might be undesirable. Similarly, given that smaller boll size has been associated with smaller seed and lower seedling vigor (Bridge et al., 1971; Calhoun and Bowman, 1999), the apparent shift in distribution of the RI lines toward the smaller boll size of the introgressed NM24016 parent might be detrimental. The reported positive association of smaller boll size with higher yield (Miller and Rawlings, 1967; Bridge et al., 1971) was not observed in the current investigation. However, taller plant heights were positively associated with higher yield in the population. Approximately 15% of the RI lines produced lint yields equivalent to or better than the higher yielding TM-1 parent.

Although the RIL population is composed of stable introgressed lines, it is interesting to note that the population deviates from normal distribution and exhibits large numbers of transgressive segregate lines for the traits plant height and fiber micronaire—two traits that exhibit large degrees of heterosis in F_1 interspecific hybrids of the *G. hirsutum* and *G. barbadense* species (Marani, 1964; Marani, 1968; Davis, 1978). Other traits displaying significant numbers of transgressive segregant lines include lint percentage and 2.5% span length. Lacape and Nguyen (2005) report similar transgressive segregation for pubescence among individual plants of a *G. hirsutum* × *G. barbadense* BC₂ cotton population, which they attributed to epistasis and/or complementary gene action. Tanksley et al. (1996) have discussed the possibility of new allelic combinations in interspecific progenies of mosaic genome constitution. In the case of the NM24016/TM-1 RIL population, interactions

would be interlocus, as individual loci theoretically should be homozygous.

The 98 RILs have been genotyped by RAPD (random amplified polymorphic DNA), SSR (simple sequence repeat, microsatellite), and AFLP (amplified fragment length polymorphism) markers to produce an integrated genetic map (Zhang et al., 2005). A total of 177 DNA markers have been assigned to 23 linkage groups to date. A preliminary QTL analysis using across location and year trait means has identified over 60 QTL for lint yield (16), boll size (5), plant height (3), fiber length (7), strength (13), elongation (9), and micronaire (14). Efforts to place more markers on the population map and conduct in-depth QTL analyses continue. All phenotypic data collected for the population is being placed in the CottonDB database (<http://cottondb.tamu.edu>; verified 9 February 2006) for general use by the cotton research community, and seed samples of lines will be made available through a public release.

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